

Volume 22: 75–87 Publication date: 16 August 2019 dx.doi.org/10.7751/telopea13084



plantnet.rbgsyd.nsw.gov.au/Telopea • escholarship.usyd.edu.au/journals/index.php/TEL • ISSN 0312-9764 (Print) • ISSN 2200-4025 (Online)

Recircumscription of *Prostanthera denticulata* R.Br. (Lamiaceae, Westringieae) and the new species *P. crocodyloides* T.C.Wilson

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Abstract

Recircumscription and lectotypification of *Prostanthera denticulata* R.Br. is accompanied by description of the new species *P. crocodyloides* T.C.Wilson, which is known from the south-eastern region of New South Wales, Australia. The descriptions for both taxa are accompanied by diagnostic illustrations, an updated section of the Flora of New South Wales key to *Prostanthera* and notes on distribution, habitat, and conservation status.

Introduction

Prostanthera Labill. is the largest genus of endemic Australian Lamiaceae, consisting of *c*. 94 species of woody subshrubs or small trees that grow in rocky outcrops and other well-drained habitats of the temperate mainland (Conn 1988; Wilson *et al.* 2017). Uncertainty regarding the number of *Prostanthera* species is in part due to taxon boundaries that have not yet been clearly defined. Taxa particularly affected by a lack of definition are *P. denticulata* R.Br., *P. lasianthos* Labill., *P. melissifolia* F. Muell., *P. nivea* Cunn. ex Benth., *P. ovalifolia* R.Br., *P. ringens* Benth., and *P. saxicola* R.Br. (Conn 1999).

During conservation surveys for the rare species *Zieria obcordata* A.Cunn. (Rutaceae), a collection of an unknown *Prostanthera* (*P. Carmen 453 & C. Hook*, 30 August 2011) was made from the Rock Forest area, northwest of Bathurst, New South Wales. These specimens were similar to specimens of *P. denticulata* collected by Allan Cunningham in 1822 near Bathurst (Cunningham 1822). *Prostanthera denticulata* is a robust, aromatic shrub with a characteristically scabrous texture and grows in woodlands and forests of New South Wales and Victoria. However, since taxonomic limits are unclear for *P. denticulata*, further comparative investigation was made between the collections near Bathurst and those of *P. denticulata* across its geographic range, including the type collections made by Robert Brown.

Robert Brown (1810) described *P. denticulata* based on specimens collected from the head of Middle Harbour, Sydney, New South Wales. In his Prodromus (1810), his diagnosis reads '*P. denticulata* has scabrous branches; linear leaves with a recurved, denticulate margin, glabrous adaxial surface and glandular abaxial surface; and pilose calyces'. Bentham (1870) later determined that the leaf margin on the specimens was entire, and that it only appeared denticulate because of enlarged tuberculate prickles which, when numerous, enhance the distinctively

scabrous or echinate characteristic of this species (Conn 1992, PlantNET). Bentham also broadened Brown's concept of *P. denticulata* to include other specimens with scabrous stems and falsely denticulate leaves with a linear or ovate (including broad-lanceolate) lamina from inland New South Wales (Cunningham's Bathurst collections) and Victoria (from Grampians National Park in the west to Mt Buffalo National Park in the east). While doing so, Bentham (1870) recognised the difference between Cunningham's collections and the others, indicating they have narrow and long (to *c.* 2.5 cm) linear leaves with tuberculate prickles, whereas most of Brown's Port Jackson specimens, and all those across Victoria have 'broad-lanceolate' (i.e. narrow-ovate) to ovate leaves usually scarcely exceeding *c.* 0.6 cm and have few to no tuberculate prickles. He also noted the outstanding variability in inflorescence morphology that all of these forms shared: in the diminutive form, the inflorescence is a monadic uniflorescence (*i.e.* consisting of a single flower), giving a plant the appearance of having flowers in an 'axillary' position; in its larger form, it is a bracteose blastotelic racemiform conflorescence, giving a plant the appearance of having a 'racemose' inflorescence; see Conn's (1984) interpretation of the *Prostanthera* inflorescence based on Briggs and Johnson (1979). In the latter inflorescence type, flowers are subtended by ovate, acuminate coloured pherophylls, and the flowers are always nearly sessile.

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The scabrous texture, ovate to narrow-ovate leaf lamina, and variable inflorescence morphology makes *P. denticulata s. lat.* difficult to distinguish from many other aromatic shrubby species of *Prostanthera* that are scabrous (viz. *P. decussata* F.Muell., *P. granitica* Maiden & Betche, *P. hirtula* F.Muell., *P. howelliae* Blakely and *P. stricta* R.T.Baker). It appears that this has resulted in many misidentifications, judging from the range of determinations on duplicates of the same collections that we have found when examining specimens lodged at CANB, MEL and NSW. *Prostanthera denticulata s.lat.* can be distinguished from all these species by having nearly glabrous (not hirsute) adaxial leaf surfaces combined with an often 'racemiform' inflorescence (rather than appearing 'axillary', which is always a characteristic of *P. decussata*, *P. granitica*, and *P. howelliae*). Moreover, the molecular phylogeny of *Prostanthera* demonstrates that *P. denticulata s.lat.* is polyphyletic: an accession of *P. denticulata* from the Royal National Park, and another from Goonoo National Park (originally misidentified as *P. howelliae*), were not recovered within a monophyletic clade (Wilson *et al.* 2012). Furthermore, neither sample was recovered with *P. decussata*, *P. granitica*, *P. hirtula*, or *P. howelliae*, supporting the hypothesis that *P. denticulata s.lat.* comprises more than one species.

This paper provides a detailed description of *P. denticulata s.str.* that establishes a clearer species concept based on Brown's specimens. We demonstrate that the coastal *P. denticulata s.str.* is distinct from *P. denticulata s.lat* found elsewhere in New South Wales and Victoria. Brown made numerous collections of *P. denticulata* and did not specify a holotype. Therefore, we designate one of Brown's collections made at the head of middle harbour, Port Jackson, as lectotype.

Through the process of comparing specimens of *P. denticulata s.lat.*, it became apparent that the *Prostanthera* collections from northwest of Bathurst were similar to specimen collections made from the New South Wales regions around Medway, Temora and West Wyalong. Some of these specimens had not previously been identified, while others were identified as either *P. denticulata* or *P. hirtula*. These populations share several characters not observed in other *Prostanthera*, including *P. denticulata s.str.* and other populations previously identified as *P. denticulata s.lat.*, and are here described as the new species *P. crocodyloides* T.C.Wilson. The remaining populations across Victoria and New South Wales previously considered as *P. denticulata s. lat.* will require further research to identify taxonomic boundaries and to determine whether they are sufficiently distinct from other similar eastern Australian mainland taxa (*viz. P. decussata, P. granitica, P. hirtula*, *P. howelliae*, *P. parviflora* and *P. stricta*).

Illustrations, notes regarding conservation status and geographic distribution, and changes to the key for New South Wales *Prostanthera* (on PlantNET) are provided for *P. denticulata* and *P. crocodyloides*. Descriptive terminology for the inflorescence structure is based on that of Briggs and Johnson (1979) and Conn (1984). The geographic distribution described for both species uses the defined areas based on the botanical divisions of New South Wales (Anderson 1961; Jacobs and Pickard 1981).

Taxonomy

Prostanthera denticulata R.Br. Prodromus Flora Novae Hollandiae 509 (1810).

Diagnosis: *Prostanthera denticulata* is morphologically similar to *P. hirtula*, as it has an open shrubby habit, frondobracteose racemiform conflorescences with flowers subtended by pherophylls, a flower type with reflexed adaxial lobes, anthers that do not translocate in anthesis, and anther appendages shorter than the anther. *Prostanthera denticulata* differs from *P. hirtula* by the former's typically scrambling habit (vs. typically erect habit), stems with antrorsely pointed, geniculate trichomes up to 1 mm long (vs. stems with long patent or spreading trichomes between 1 and 2 mm long), leaves pubescent or nearly glabrous with adaxial leaf

surface moderately covered by tuberculate tooth-like trichomes and sometimes hair-like trichomes (vs. hirsute with long, hair-like, ± rigid trichomes).

Lectotype (designated here): New South Wales: Head of Middle Harbour, Sydney (Port Jackson). February 1805 (printed label upper left of sheet), 'Calcanthera scabra Head of Middle Harbour P Jackson 1805 Feb' (handwritten label upper left of sheet), 'Plants of Australia Collected by Robert Brown 1801–1805 Prostanthera denticulata R. Br. (Type Collection)] BM 001041043! Probable isolectotypes: 'Prostanthera scabra Port Jackson' (handwritten label top of sheet), 'Plants of Australia Collected by Robert Brown 1801–1805 Prostanthera denticulata R.Br. (Type Collection) New South Wales: Head of Middle Harbour, Sydney (Port Jackson). February 1805' (printed label left of sheet), 'N. Hollandia, Pt Jackson R Brown' (handwritten label bottom of sheet), BM 001041044!; 'Prostanthera denticulata (P. scabra Hb Br.) var? Middle Harbour' (handwritten label lower left of sheet), 'Herb. Mus. Paris. Prostanthera denticulata R.Br. Australie Robert Brown. Envoi du Jardin Royal de Kew. Reçu le 19 Janvier 1884.' (handwritten lower right of sheet), P 00686281!'; 'Prostanthera scabra Port Jackson' (handwritten label bottom right of sheet), 'Plants of Australia Collected by Robert Brown 1801–1805 Prostanthera denticulata R.Br. (Type Collection) New South Wales: Head of Middle Harbour, Sydney (Port Jackson). February 1805' (printed label bottom right of sheet), CANB 278983!.

Open, scandent to semi-erect, woody shrub to c. 1 m tall, sometimes evenly covered with large multi-cellular sessile hemispherical glands (c. 0.1 mm wide) and small sessile glands (to 0.03 mm wide), aromatic with scent combination of pine and cineole when crushed. *Stem* developing greenish or yellowish-brown bark. *Branchlets* rounded, or slightly square in cross section, yellowish green, densely covered with short antrorse, geniculate, scabrous hairs (0.05–0.5 mm long; 1–20 hairs/mm²), multicellular sessile glands absent to occasional, small sessile glands (to 5 glands/mm²). Leaves discolorous; petiole 0.3–1.4 mm long; lamina narrow ovate to ovate (appearing narrower when dry), (2–)7–24 mm long, 1–5 mm wide, base shortly attenuate to truncate, margin entire or slightly undulate and weakly to strongly recurved, apex acute to obtuse; abaxial surface pale green, midvein prominent, covered with antrorse to spreading hair-like trichomes 0.05–0.4 mm long with a density 1–4(–11)/mm², multicellular sessile glands 1–5/mm², without small sessile glands; adaxial surface mid-green, secondary veins indistinct, stiff to tooth-like trichomes 1-7/mm² and 0.05-0.2(-0.3) mm long, hair-like trichomes along margin to 0.02-0.15 mm long. Inflorescence a frondobracteose racemiform conflorescence, uniflorescences monadic, 8–60 mm long and consisting of 1–5 nodes, axis green to dark maroon, indumentum as stem. Pherophylls resembling variously-reduced leaves, caducous, ovate, 1-4.5 mm long, 0.7-2 mm wide, indumentum similar to vegetative leaves, mid-green to completely dark maroon. Podium 1-2.1 mm long, indumentum similar to inflorescence axis, propodium to anthopodium ratio 2-9. Prophylls persistent, inserted slightly to distinctly sub-opposite, strongly narrow ovate to linear, 0.35–1.7 mm long, 0.1–0.3 mm wide, indumentum and colour similar to podium. Calyx bilobed, margin entire, mid-green to completely dark maroon; inner surface densely covered with short hairs (0.02–0.07 mm long; 40–80/mm²); outer surface moderately covered with patent trichomes (0.07–0.46 mm long, 2–10(–12)/mm²), and multicellular sessile glands (2-6/mm²); tube 1.4-1.9 mm long; abaxial lobe broadly ovate, 2.7-3.4 mm long, 1.6-2.8 mm wide, apex rounded, base truncate; adaxial lobe ovate to broadly ovate (0.7–1.6 mm long, 2.6–5.2 mm wide). Corolla 8.5–15 mm long, mauve with no markings, outer surface glabrous or with few trichomes on adaxial surface of tube, lobes with large sessile glands 2–12/mm² more dense distally, lobe margins erose; tube 5–7 mm long and up to 4–6 mm wide, campanulate, inner surface glabrous; abaxial median lobe weakly spathulate, 3.3–5 mm long, base 1.8–2.8 mm wide, 4.1–5.7 mm wide near apex, apex rounded, ± emarginate (sinus to 0.8 mm long and 1.5 mm wide); lateral lobes oblong to weakly obovate, 2.3–4 mm long, 2.1–4.3 mm wide, apex obtuse; adaxial lobes fused into an adaxial median-lobe pair, separated by a broad shallow medial sinus to 0.5–1.5 mm long, each lobe 1.4–2.1 mm long, 3.2–5.2 mm wide, apex depressed ovate or truncate. Stamens didynamous, inserted 1.6–2.0 mm above corolla base, pollen sacs divergent, dark purple; abaxial stamens filament 1–2.1 mm long and c. 0.3 mm wide, anther 1.2–1.4 mm long and 1–1.5 mm wide, connective extended to form a basal appendage adjacent to abaxial locule (to 0.5 mm long, sometimes absent) and a basal appendage adjacent to adaxial locule (0.1–0.5 mm long) terminating in deltoid trichomes up to 0.1 mm long; adaxial stamens filament 0.9–1.3 mm long and c. 0.3 mm wide, anther 1.1–1.2 mm long and 1.1–1.4 mm wide, connective extended to form a basal appendage adjacent to abaxial locule (0.1-0.3 mm long) and adjacent to adaxial locule (0.1-0.6 mm long)terminating in deltoid trichomes up to 0.1 mm long. *Gynoecium* ovary 0.3–0.45 mm long and 0.6–0.9 mm wide, disc 0.15–0.3 mm long; style 5.5–8 mm long; abaxial stigmatic lobe longer (0.45–1 mm) than adaxial lobe (0.2–0.9 mm). *Fruiting calyx* beige when senesced; tube 1–1.2 mm long; abaxial lobe 2.7–3.4 mm long and 2.6–3.4 mm wide; adaxial lobe 0.7–1.3 mm long and 3–4 mm wide. *Mericarps* 1.3–1.9 mm long and to c. 1 mm wide, distally extended to 0.5–1.3 mm beyond base of style, wrinkled, light brown to beige. *Flowering* between October to December, although sporadic flowering can occur at any time if conditions are optimal. Figs 1 & 2. 78

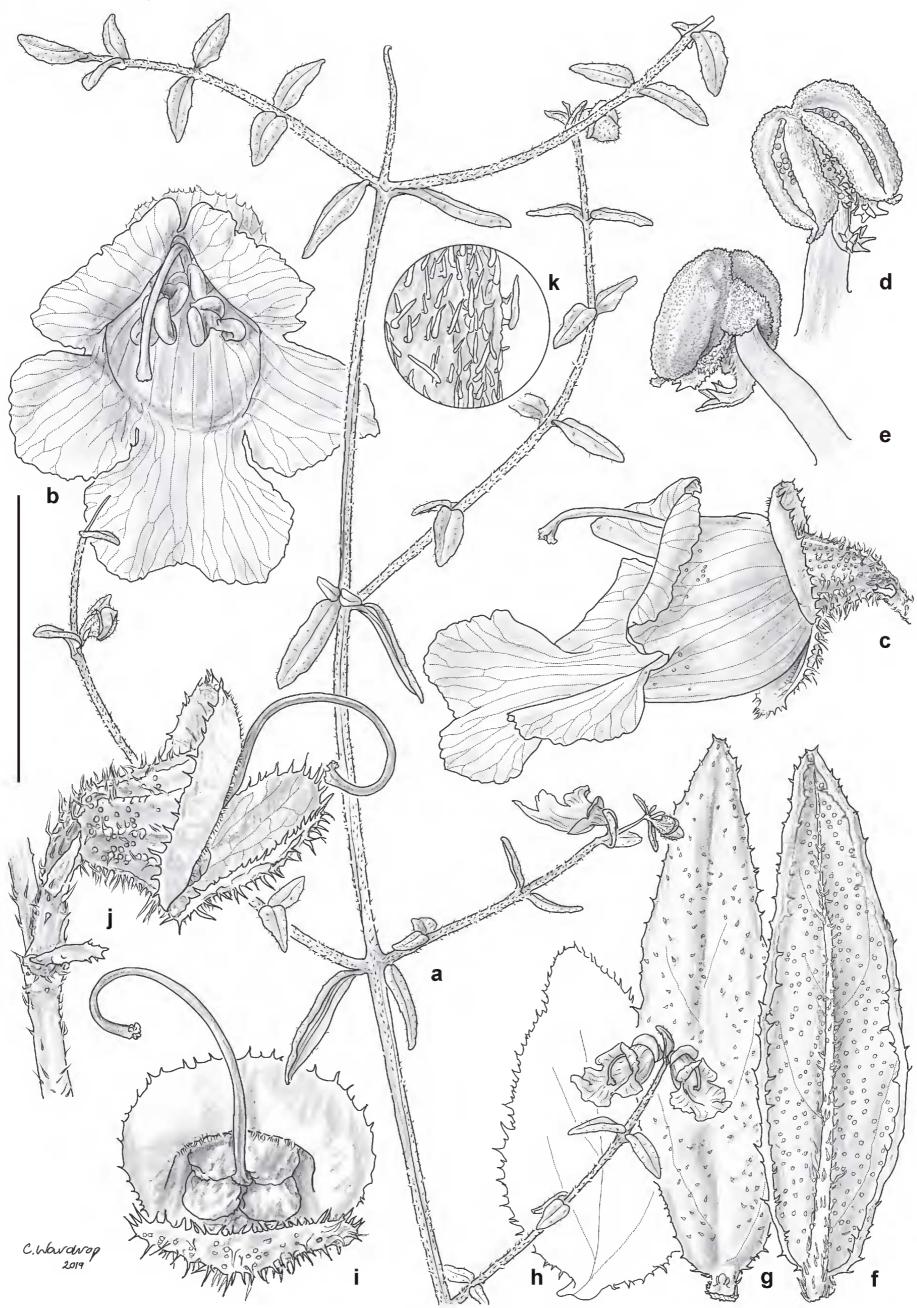


Fig. 1. *Prostanthera denticulata*. a. habit and inflorescence; b. corolla (front view) showing relative position of stamens and style; c. flower (lateral view), showing short prophylls, calyx, corolla and pistil; d. adaxial anther, ventral view showing both longer (left) and shorter (right) appendages emerging from the connective between locules; e. adaxial anther, oblique dorsal view; f. leaf, abaxial view; g. leaf, adaxial view; h. leaf, silouette of adaxial view; i. fruiting calyx (front view); j. fruiting calyx (lateral view) showing prophylls. Scale bar: a = 4 cm; b,c,f-h = 0.75 cm; d,e = 0.25 cm; i,j = 0.6 cm; k=0.2 cm. Material: NSW901656, *T.C. Wilson 398, T.C. Wilson 241* and *G. Taseski 777*. Illustrations: C. Wardrop

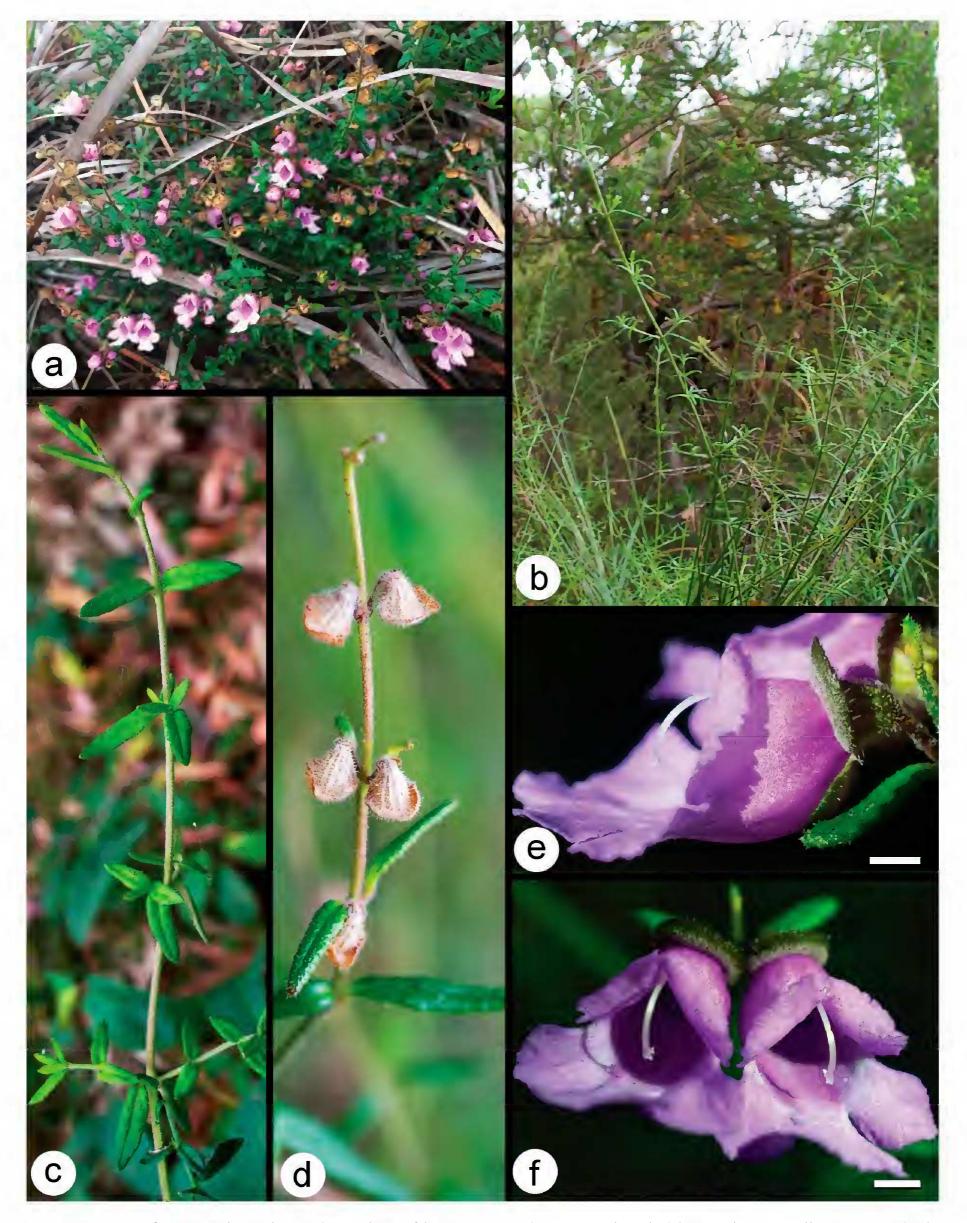


Fig. 2. Images of *Prostanthera denticulata* taken of living material associated with (a) Taseski 777 collection at Bilgola headland, (b–d) Wilson 241 collection at Royal National Park; (e,f) Wilson 328 collection at McKay Nature Reserve, Sydney. **a**, semi-prostrate subshrub growing in heath on coastal slope; **b**, sprawling open shrub in heathy woodland; **c**, vegetative shoot; **d**, racemose infructescence with persistent pherophylls subtending fruiting calyces at the second node from base; **e**, profile of flower; **f**, front view flowers. Scale bar: e,f = 2 mm. Photographs: G. Taseski (a) and T.C. Wilson (b–f).

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Specimens examined: AUSTRALIA: NEW SOUTH WALES: Central Coast: Bouddi National Park: Gerrin Track, 150 m N of lookout to Maitland Bay, near Putty Beach end, V. Williams 1, 10 October 1987 (NSW); Kincumber: Corner of Avoca Drive along back fence of Kincumber Public School, D. Warman s.n., 27 August 2005 (NSW); Cowan: Cowan Creek, W. Blakely & D. Shiress s.n., November 1918 (NSW); W. Blakely s.n., November 1918 (NSW); W. Blakely s.n., 8 November 1936 (NSW); Cedar Creek, W. Blakely & D. Shiress s.n., 12 September 1926 (NSW); Sydney: Bush on top of Palm Beach Isthmus, R. Goode 358, 30 September 1961 (NSW); Kuringai, M. Welch & D. Cannon s.n., October 1922 (NSW); Church Point, M. Tindale s.n., September 1945 (NSW); Church Point Road, D. Tuckson s.n., 18 October 1956 (NSW); Towlers Bay, West end of Towlers Bay, M. Fletcher s.n., 2 October 1971 (NSW); Beside track to Pittwater Youth Hostel from Halls Wharf, J. Scott 1, 22 November 1989 (NSW); McKay Nature Reserve, T. Wilson 398, 26 October 2012 (NSW); Bilgola Head, A. Morris s.n., 26 September 1927 (NSW); G. Taseski 777, October 1 2018 (NSW); A. Rodd 3540 & M. Watson, 4 November 1980 (NSW); Bayview, E. Constable, 20 January 1948 (NSW); Mona Vale, In gully to the south of 95 Cabbage Tree Road, R. Johnstone 131 & C. Colton, 5 November 1988 (NSW); Katandra Bushland Sanctuary, T. James 541 & R. Coveny, 20 September 1984 (NSW); R. Coveny 9693, 19 October 1977 (NSW); Duffy's Forest, Lot 88 Eurabba Road, R. Palsson 55 & A. Rodd, 22 August 2017 (NSW); Newport, R. Selfe s.n., October 1910 (NSW); J. Fletcher s.n., August 1887 (NSW); North shore of Narrabeen lake, L. Johnson s.n., 5 October 1946 (NSW); War Veteran's village Narrabeen Lakes adjacent to Jamieson Park and Narrabeen Lake, N. Skelton 94002, 4 December 1994 (NSW); South Turramurra, I. McAllan s.n. 3, October 2001 (NSW); Manly Beach, Woolls s.n., 15 January 1807 (MEL, NSW); Loftus: J. Camfield s.n., October 1894 (NSW); J. Camfield s.n., October 1898 (NSW); Port Hacking River: J. Camfield s.n., December 1898 (NSW); Royal National Park: Along the Basin Lagoon track from Bonnie vale campground, T. Wilson 241 & K. Gibbons, 23 Februrary 2011 (NSW); Otford: R. Collie s.n., 3 November 1888 (NSW); Garrawarra Reserve: E. Jacobs s.n., 20 October 1907 (NSW).

Recognition: For characters differentiating *P. denticulata* from similar species see Table 1.

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Table 1. Comparison of selected morphological characters that can be used to distinguish between *Prostanthera crocodyloides* and its most similar congeners. Additional information for *P. cryptandroides* sourced from Conn 1999.

Characters	P. crocodyloides	P. denticulata	P. cryptandroides	P. hirtula
Glandular trichome location	inflorescence, flowers (not corolla) and sometimes leaf petioles	absent	stems, leaves and inflorescences (in subsp. euphrasioides only)	absent
Stem trichomes	Patent or spreading	Geniculate and antrorse	Patent or spreading	Patent or spreading
Tooth-like trichomes	to 0.5 mm long	to 0.2(-0.3) mm long	absent	absent
Leaf margin	entire	entire	lobed	entire
Leaf large tubercules	present	present	absent	present
Leaf lamina length	8–20 mm	7–24 mm	6–9 mm	10–30 mm
Inflorescence	flowers usually on racemiform conflorescences (sometimes appearing axillary); to 8 nodes	flowers usually on racemiform conflorescences (sometimes appearing axillary); 1–3(–4) nodes	flowers appearing axillary	flowers usually on racemiform conflorescences (sometimes appearing axillary); to 8 nodes
Pherophyll	hastate	ovate	generally absent	ovate
Prophyll	1.4–5 mm long; often recurved	1.3–1.7 mm long; straight	4–5 mm long; straight	to 3 mm long; straight
Calyx	Hirsute, with glandular trichomes	hirsute	glabrous to hirsute	hirsute
Corolla	mauve with no markings	mauve with no markings	pale mauve with orange markings in throat	mauve with no markings
Largest anther appendage length: anther locule length ratio	<0.5	<0.5	>1	<0.5

Notes: The specimen BM00 1041043 is here chosen as the lectotype because it has the greatest amount of reproductive material from all of Robert Brown's associated gatherings. Flowers of *P. denticulata* are chasmogamous: both female and male functions overlap to some extent during anthesis, but the stigma is exserted and porrect (with respect to the corolla) while stamens are found within the corolla tube (Fig. 2). This physical separation of sexes is expressed in other closely related species of *Prostanthera* (Wilson *et al.* 2012), and the flower type can be used to distinguish *P. denticulata* from several other species that have a dichogamous flower (Wilson *et al.* 2017).

The pollinators of *P. denticulata* are not known, but from the flower type, it could be inferred that they are insect pollinators belonging to Diptera, Hymenoptera, and Coleoptera (Wilson *et al.* 2017).

Distribution: *Prostanthera denticulata* is known from the Central Coast, New South Wales, as far north as Bouddi National Park and as far south as Royal National Park (Fig. 3).

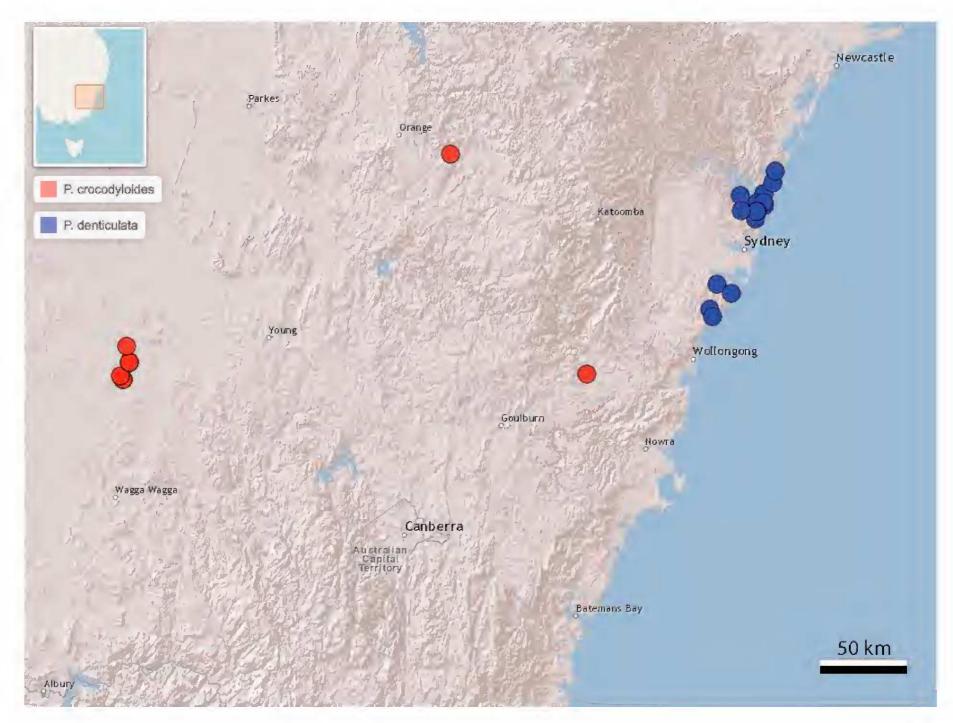


Fig. 3. The known locations of *Prostanthera crocodyloides* (red) occur west of all known locations of *P. denticulata* (blue) in New South Wales, Australia.

Habitat: Steep to gentle slopes (between 0–200 metres) in sandy, gravelly, well-drained soils derived from Triassic coarse-grained sandstone. Surrounding vegetation typically has heath-like elements in woodland or wet sclerophyll forest.

Conservation status: Populations of *P. denticulata* occur within National Parks and other conservation areas, but several populations may be threatened by adjacent areas of urban growth around the greater Sydney area. Based on the number of collections and our understanding of the contemporary distribution for this species, there are approximately ten existent disjunct populations that fit an area of occupancy of less than 500 km². No study has extensively surveyed this species and so population numbers are unknown. Based on this evidence, the species might be suitable for an IUCN Redlist (IUCN 2019) endangered or vulnerable listing if any future evidence demonstrates a continuous decline or extreme fluctuation at any demographic level. However, since historical data for populations of *P. denticulata* are not known, this species should be listed as data deficient (IUCN 2019).

Prostanthera crocodyloides T.C.Wilson, sp. nov.

Diagnosis: *Prostanthera crocodyloides* is similar to *P. denticulata*, as it has an open shrubby habit, scabrous leaves bearing distinct tooth-like hairs, and a flower type with reflexed adaxial lobes, anthers that do not translocate in anthesis, and anther appendages shorter than the anther. *Prostanthera crocodyloides* differs from *P. denticulata* by its patent or spreading trichomes and regularly distributed sessile glands on branchlets (vs. the latter's geniculate antrorse trichomes and occasionally distributed sessile glands), adaxial leaf surface with tuberculate tooth-like trichomes to 0.5 mm long (vs. rarely to 0.3 mm long), frondobracteose racemose conflorescence

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with flowers subtended by hastate pherophylls (vs. subtended by ovate acuminate pherophylls), generally longer prophylls 1.4–5 mm long (vs. to 1.7 mm long), glandular trichomes associated with inflorescence axis, pherophylls, prophylls, and calyces (vs. glandular trichomes absent).

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Type: Australia: New South Wales: Central Tablelands: Bathurst: Crackerjack Rock, *T.C. Wilson 757, P. Carmen, C. Hook, M.A.M. Renner, D. Shelly*, 28 Nov 2016 (holotype: NSW 997626 isotypes: CANB, MEL).

Open, erect, woody shrub to 2 m tall, crown to c. 1.5 m diam., evenly covered with large multi-cellular sessile hemispherical glands (c. 0.1 mm wide) and either small sessile glands (to 0.05 mm wide) or glandular hairs (to 0.4 mm long), strongly aromatic with scent combination of pine and cineole when lightly brushed or crushed. Stem to 5 cm diam. near base of shrub. Branchlets rounded, yellowish green, densely covered with short patent or spreading trichomes (0.02–0.2 mm long; (3–)20–50 trichomes/mm²), moderately covered by multicellular sessile glands (up to 4 glands/mm²) and small sessile glands (1–)5–10 glands/mm²; bark smooth and waxy, greyish brown with horizontal yellow- or red-brown bands, and vertical lenticel-like openings on lower stem and older branches. Leaves discolorous; petiole absent or when present 0.3-0.8 mm long, sometimes with a few glandular trichomes; lamina linear to very narrowly ovate or elliptic, 8-20 mm long, 0.6-2 mm wide, base shortly attenuate to truncate, margin entire and weakly to strongly recurved, apex obtuse; abaxial surface pale yellowish-green, midvein prominent, densely covered with patent 0.01–0.2 mm long hair-like trichomes (20-50(-80) trichomes/mm²), multicellular sessile glands 1-9 glands/mm², and small sessile glands 6-16 glands/mm²; adaxial surface mid-green, secondary veins indistinct, 0.05-0.4 mm long hair-like trichomes particularly at leaf base (up to 20-50 trichomes/mm²), small tooth-like trichomes 0.02-0.1 mm long and densely covering surface $((1-)16-25 \text{ trichomes/mm}^2)$, with larger tuberculate tooth-like trichomes (to 0.5) mm long and 0.05-0.2 mm wide, c. 1/mm²), multicellular sessile glands 1-9/glands mm², and small sessile glands 6–16 glands/mm². *Inflorescence* a frondobracteose racemose conflorescence with main axis up to c. 8 nodes; uniflorescences monadic, axis green to dark maroon, indumentum with patent hair-like and/or toothlike trichomes (0.02–0.15 mm long, 3–32 trichomes/mm²), large multicellular sessile glands 1–6 glands/mm², small sessile glands 3-24 glands/mm², and glandular trichomes absent or sparse (up to 10 trichomes/mm²) and 0.1–0.18 mm long. *Pherophylls* persistent, hastate, margin becoming weakly recurved, base broad, 0.7–10 mm long, 0.3–3 mm wide, indumentum similar to vegetative leaves, mid-green to completely dark maroon. *Podium* 0.9–1.8 mm long, indumentum similar to inflorescence axis, propodium to anthopodium ratio 0.8–5. *Prophylls* persistent, inserted slightly to distinctly sub-opposite, strongly narrow ovate to linear and sometimes recurved, 1.4–3.6(–5) mm long, 0.1–0.5 mm wide, indumentum and colour similar to podium. *Calyx* bilobed, margin entire or sometimes with adaxial lobe with three inconspicuous lobes, mid-green to completely dark maroon; inner surface glabrous; outer surface densely covered with patent trichomes (0.02–0.15 mm long, 3-32 trichomes/mm²), large glands (1-4/mm²) and glandular trichomes (to 4 mm long, 0.02-11 trichomes/ mm²), becoming more sparsely distributed distally; tube 1.6–2.6 mm long; abaxial lobe broadly ovate, 1.7–2.3 mm long, 1.8–3 mm wide, base truncate, apex rounded; adaxial lobe ovate to broadly ovate, 1.2–3 mm long, 1.8–3.6 mm wide, apex rounded. Corolla 7–10 mm long, mauve without markings, outer surface glabrous except lateral and abaxial lobes, with or without multicellular sessile glands 3–7 glands/mm²; tube 3.5–5.5 mm long, campanulate, inner surface glabrous; abaxial median lobe weakly spathulate, 2.2–3.6 mm long, 0.6–2.6 mm wide at base, 1.8–3.8 mm wide near apex, apex rounded, ± emarginate (sinus 0.16 mm long, 0.5 mm wide); lateral lobes slightly obovate, 2.1–3.3 mm long, 2.1–3.6 mm wide, apex broadly obtuse to rounded, slightly retuse; adaxial median-lobe pair deeply divided, each lobe depressed ovate, 1.7-2.7 mm long, 2.2-3.6 mm wide, with margin slightly irregular, apex obtuse to truncate, medial sinus broad and 0.2 mm long. Stamens didynamous, inserted 1.2–2.4 mm from corolla base, dark purple; staminal filaments 0.7–1.6 mm long, c. 0.3 mm wide, anthers 1.2-1.7 mm long, 0.7-1.1 mm wide; connective on all anthers extended to form a basal appendage adjacent to the adaxial locule 0.2–0.5 mm long and terminating in deltoid trichomes up to 0.1 mm long (adaxial anthers rarely with a second shorter basal appendage adjacent to abaxial locule). Gynoecium disc 0.25–0.4 mm long; ovary 0.3–0.6 mm long and 0.7–1 mm diam.; style 3.3–7 mm long; stigmatic lobes 0.16– 0.32 mm long. Fruiting calyx beige-coloured; tube 2.2–2.9 mm long; abaxial lobe 2.3–3.2 mm long, 2.6–3.5 mm wide; adaxial lobe 1.8–4 mm long, 2.5–4.2 mm wide. *Mericarps c.* 3.2 mm long, distally extended to 0.7–1.1 mm beyond base of style, wrinkled, light brown to beige. Flowering primarily between late August to November, although sporadic flowering might occur at any time depending if conditions are optimal. Figs 4 & 5.

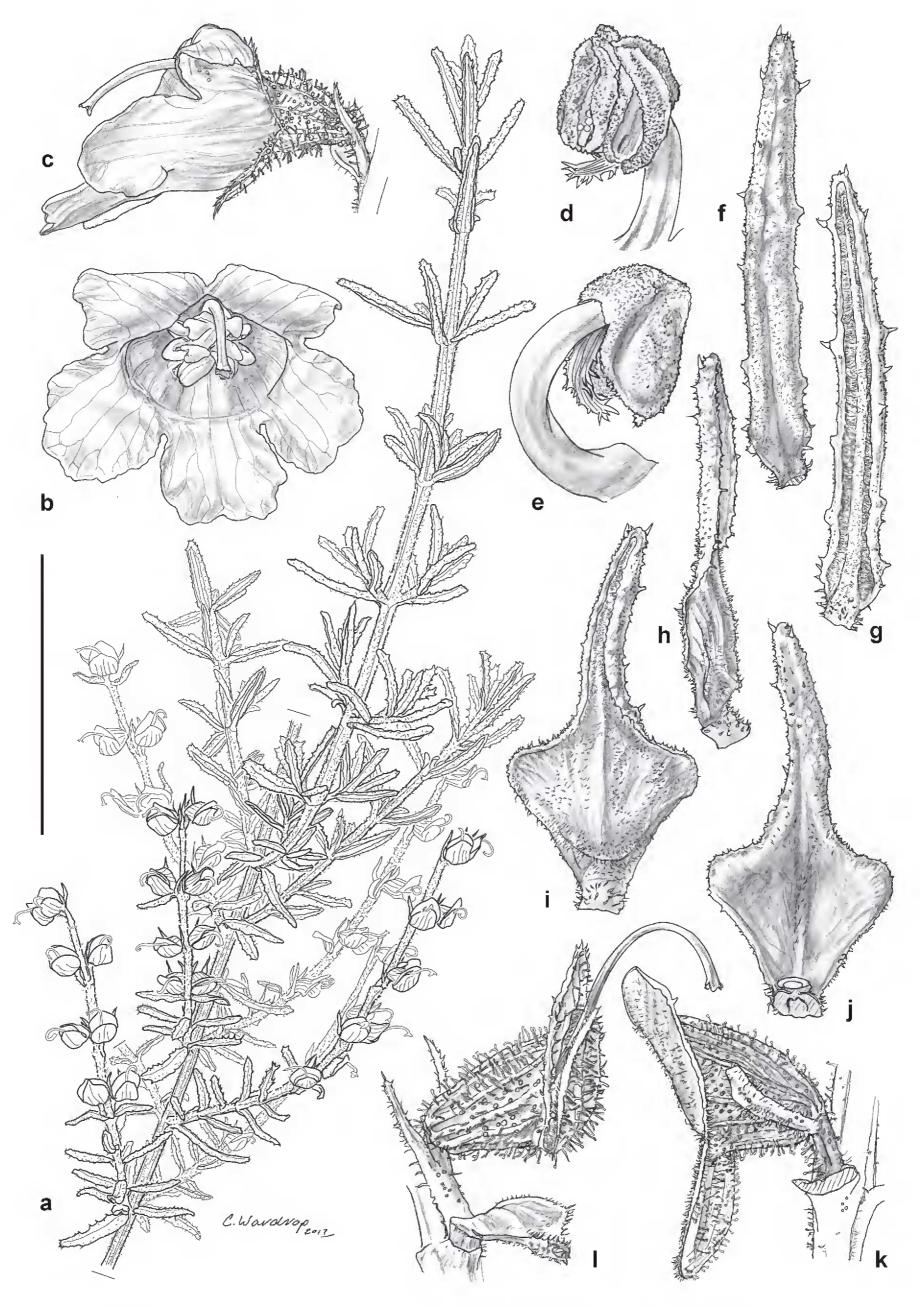


Fig. 4. *Prostanthera crocodyloides.* a. habit and inflorescence; b. corolla (front view) showing relative position of stamens and style; c. flower (lateral view), showing prophylls, calyx, corolla and pistil; d. anther, oblique adaxial view; e. anther, abaxial view; f. leaf, adaxial view; g. leaf, abaxial view with detail showing tooth-like hairs; h. pherophyll, profile view; i. pherophyll, abaxial view; j. pherophyll, adaxial view; k. flowering calyx (corolla removed) and prophylls showing detail of glandular hairs; l. fruiting calyx with prophylls subtended by pherophyll. Scale bar: a = 4 cm; b,c,f,g = 0.75 cm; d,e = 0.25 cm; h-l = 0.6 cm. Material: *T.C. Wilson 757* and *P. Carmen 453*. Illustrations: C. Wardrop.

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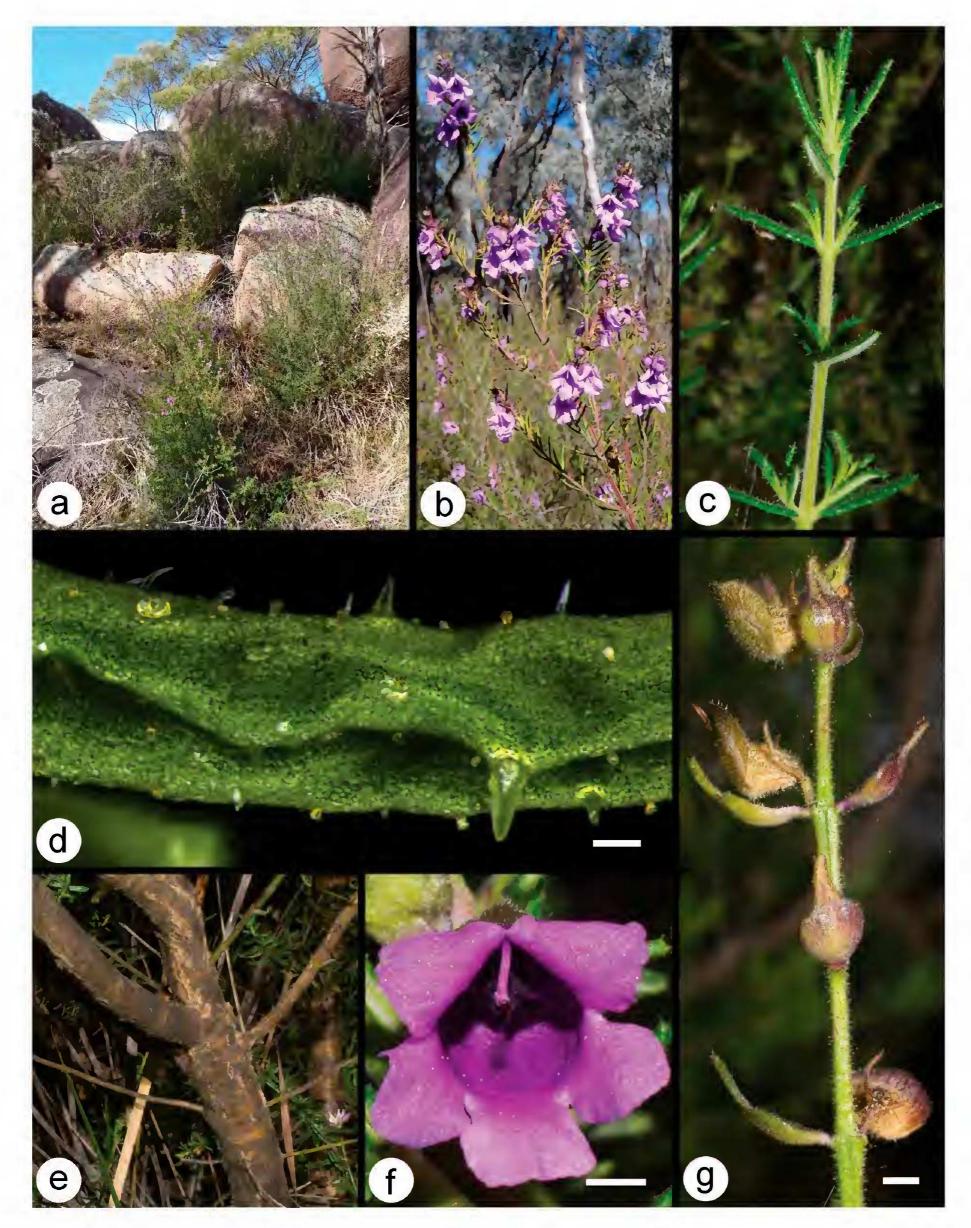


Fig. 5. *Prostanthera crocodyloides* found at Bathurst (a, c–g) and Ingalba Nature Reserve (b). **a**, growing in open woodland along slopes, amongst granite boulders and pavements (Bathurst); **b**, racemose inflorescence; **c**, vegetative shoot; **d**, dissecting micrograph of Carmen 453: abaxial surface of inflorescence leaf apex showing tooth-like trichomes, small sessile glands and a large multicellular sessile gland; **e**, stem developing smooth bark with horizontal red-brown bands; **f**, front view of anthetic flower; **g**, racemose infructescence showing hastate persistent pherophylls and fruiting calyces. Scale bar: d = 0.1 mm; f,g = 2 mm. Photographs: C.J. Hook (a,b) and T.C. Wilson (c–g).

Specimens examined: AUSTRALIA: NEW SOUTH WALES: Central Tablelands: Granitic mountains west from the Settlement of Bathurst, *A. Cunningham s.n.*, 23 Oct, 1822 (K 001097773); Rock Forest, Crackerjack Rock, *P. Carmen 453 & C. Hook*, 30 Aug 2011 (CANB, NSW); *P. Carmen 514 & C. Hook, D. Shelly*, 26 Sept 2016 (CANB, NSW); *T.C. Wilson 578*, 579, *M.A.M. Renner, P. Carmen, C. Hook & D. Shelly*, 28 Nov 2016 (NSW, CANB, MEL); Blue Mountains: *Unknown collector* (K 001097774); Medway: Medway rivulet: *B.J. Conn 2564 & R. Miller*, 13 June 1987 (NSW); *B.J. Conn 2664 & R. Miller*, 26 Oct 1987 (NSW); *M. Kennedy 155, A. Fairley, R. Miller & P. Hind*, 10 Oct 1991 (NSW); Central Western Slopes: 25 km south of West Wyalong, *P.L. Milthorpe s.n.*, 10 Aug 1974 (CANB 828400); Temora: *Rev. J. W. Dwyer s.n.*, Aug 1915 (NSW 942166); *Rev. J. W. Dwyer s.n.*, Sept 1915 (NSW 942165); 10 km west of Temora on Ariah Park Road, *J.G. Brickhill s.n.*, 13 Oct 1979 (National Parks and Wildlife Service New South Wales, Griffith); Ingalba Nature Reserve: *J. W. Wrigley s.n.*, 2 Oct 1971 (CBG 41294); *B. Muffet s.n.*, 24 August 1974 (CBG 55784); T. van den Brock *s.n.*, 2 Oct 1967 (CBG 54551); *G. Butler s.n.*, 8 Nov 1993 (CBG 9216030); Mt Wharrun area, *J.G. Brickhill s.n.*, 16 Aug 1978 (CANB 832370); walking track to Mt Wharrun, *P. Carmen 537 & C. Hook*, 9 Sept 2017 (CANB); north eastern corner, *P. Carmen 539 & C. Hook*, 10 September 2017 (CANB); Big Bush Nature Reserve: *J. Schlunke s.n.*, May 2011 (NSW 1004346).

Recognition: The combination of a frondobracteose racemose conflorescence and monadic uniflorescences, glandular hairs and hastate pherophylls makes *P. crocodyloides* distinct from other species of *Prostanthera*, including *P. denticulata*. *Prostanthera crocodyloides* can also be distinguished from *P. denticulata* by more densely distributed tuberculate hairs and glandular trichomes associated with inflorescence stems, pedicels and calyces. *Prostanthera hirtula* can have scabrous leaves and has similar-looking racemiform conflorescences, although *P. crocodyloides* can be distinguished from *P. hirtula* by being covered by distinctive tuberculate, tooth-like trichomes (vs. hair-like trichomes), hastate pherophylls (vs. ovate pherophylls) and glandular trichomes (vs. glandular trichomes absent). The distinctive glandular trichomes borne at highest density on *P. crocodyloides* inflorescences and flower parts might lead to confusion with *P. cryptandroides* A.Cunn. ex Benth. *Prostanthera crocodyloides* is unlike *P. cryptandroides* subsp. *cryptandroides* because the leaf margin is entire (vs. dentate leaves) and anther appendages are shorter than the anther locule (vs. longer than the anther locule). *Prostanthera cryptandroides* subsp. *euphrasioides* (Benth.) B.J.Conn is unique because it has glandular trichomes in high density over vegetative parts such as leaves that are not scabrous. Further information on similarities and differences between the above species is summarised in Table 1.

Notes: Glandular trichomes that are found on reproductive parts of *P. crocodyloides* appear to be homologous with the small sessile glands (not larger hemispherical glands) that are distributed over vegetative parts. There usually is a gradient in the mature length of these glands, and the later developing flowers and axis of the inflorescence tend to have more glandular trichomes and fewer (or absent) sessile glands. The phenology of the glandular trichomes appears to be variable across the geographical distribution of *P. crocodyloides*. Populations near Bathurst and Medway begin producing glandular trichomes earlier in reproductive development (viz. on the inflorescence axes and pherophylls) whereas populations from near West Wyalong and surrounding Temora produce glandular trichomes later (viz. on prophylls and calyces).

Flowers of *P. crocodyloides* are not protandrous, however anthers are ready to dehisce pollen and the stigma is not receptive at beginning of anthesis. Stigmas become receptive soon after flowers open and while anthers can still disseminate pollen. Flowers of this species are chasmogamous because the stigmatic tip is held distal to the anthers (Wilson *et al.* 2017): stigma is exserted and porrect (respective to the corolla) while stamens are found within corolla tube (Figs 4b & c, 5f). The pollinators of *P. crocodyloides* are not known but, based on the flower type, it would be expected that a high diversity of insects are potential pollinators, including members of Diptera, Hymenoptera and Coleoptera (Wilson *et al.* 2017). It is likely that the anther appendage of this species increases the potential for visitors to disrupt the anthers and thereby release pollen, which is the pollination mechanism that has been observed in other *Prostanthera* (Wilson *et al.* 2017). Although sometimes a second, smaller appendage is found associated with the abaxial locule, *P. crocodyloides* is typically distinguished from *P. denticulata* by having only one appendage (not two) per anther.

Etymology: The specific epithet 'crocodyloides' refers to several crocodilian-like qualities on the leaves. Microscopic examination of a leaf reveals small to large (up to 0.4 mm long) tooth-like trichomes on tubercules, resembling a crocodile tooth. The recurved margin (or strongly recurved to revolute when desiccated) of the narrow-ovate leaf gives the likeness to a crocodile's upper mandible, especially when the large tooth-like trichomes are distributed on its length (Fig. 5d). The tubercules over the adaxial surface of the leaf also gives the appearance and tactile quality of crocodilian skin.

Distribution: *Prostanthera crocodyloides* is known from five populations across the Central Tablelands and Central Western Slopes, New South Wales: 1) Crackerjack Rock, Rock Forest northwest of Bathurst; 2) West Wyalong area; 3) Ingalba Nature Reserve; 4) Big Bush Nature Reserve; 5) Medway rivulet adjacent to Belanglo State Forest (Fig. 3).

The northernmost population of *P. crocodyloides* is on a western slope of private property in the Rock Forest locality near Bathurst. It consists of approximately 250 individuals in three loosely-disjunct sites covering an area of one km². The *P. crocodyloides* population from south of West Wyalong was not able to be relocated for this study. Based on our field surveys conducted in 2017 and 2018, and by Porteners (2001), *P. crocodyloides* occurs in two areas within Ingalba Nature Reserve. One area is in the northern part of the Reserve, either side of the Temora-Ariah Park Road, and the second is in the southern part of the Reserve near Mt Wharrun. Each site was estimated to contain over two thousand individuals in small to extensive patches. There are four sites reported in the vicinity of the Big Bush Nature Reserve, three in the reserve (J. Schlunke pers. comm.) and a fourth on adjacent private property. The south-eastern population at Medway is known from two collections with specific locality details; another specimen (K 001097774) from an unidentified collector in Hookers' herbarium is only labelled with the locality of Blue Mountains and might refer to the Medway locality, or to an additional unknown population in the Blue Mountains Wilderness.

Habitat: Outcrops, steep to gentle slopes, and pavements (between 400–930 metres), growing in heathy shrubland to open woodland. Grows in sandy, gravelly, well-drained soils derived from a wide range of geologies: Carboniferous coarse-grained porphyritic felsic granite at Rock Forest (Dunkeld Granite: gmaps. geoscience.nsw.gov.au; Briggs and Leigh 1990); Ordovician siltstone, sandstone, quartz-mica schist, minor graphitic schist, and hornfels (Wagga Group: gmaps.geoscience.nsw.gov.au) at Ingalba and Big Bush Nature Reserve; Hawkesbury sandstone at Medway.

Conservation status: Two of the five separate populations of *P. crocodyloides* are located in Nature Reserves. Two sites in a population located at Ingalba Nature Reserve contain over 2000 individuals each, and one site in the population at Big Bush Nature Reserve contains over 500 individuals. A comprehensive search at the Rock Forest population counted 251 individuals. The precise location and status of the West Wyalong population is uncertain, and the number of individuals at the population near Medway is unknown. Given these data, there are five known populations within less than 5,000 km². There is likely no gene flow between these populations since they are disjunct, which would therefore necessitate conservation for each one. Based on this evidence the species could merit an IUCN Redlist (IUCN 2019) endangered listing if any further evidence is provided to demonstrate a continuous decline or extreme fluctuation at any demographic level. However, until historical data for these populations are provided, *P. crocodyloides* should be listed as data deficient (IUCN 2019).

Updated key to species

Sections of the key to the species of *Prostanthera* (Conn and Wilson 2015) occurring in New South Wales are here amended to incorporate *P. crocodyloides* and updated information about *P. denticulata*. The current key considers *P. denticulata* as having flowers arranged in leafy botryoids (i.e. flowers appearing axillary). *Prostanthera crocodyloides* can also have flowers in leafy botryoids, and therefore couplets 40, 40a, and 40b are used to distinguish both species from *P. howelliae* and *P. decussata* F.Muell. *Prostanthera crocodyloides* and *P. denticulata* also grow flowers in racemiform superconflorescences (appearing as terminal racemose inflorescences), and therefore couplets 15, 15a, and 15b are implemented to distinguish both from *P. hirtula* F.Muell. ex Benth and *P. makinsonii* B.J.Conn & T.C.Wilson. A caveat is also included in couplet 3 that large tubercules on the leaf could give the false impression of a denticulate margin. In order to be compatible with the existing key, the term 'hair' is used instead of trichome.

3	Leaves with margin entire (although may appear toothed because of tubercules on the margin)4		
	Leaves with margin variously toothed		
14	Leaves 6–10 mm wide, margins weakly recurved		
	Leaves 1–6 mm wide, margins often strongly recurved to revolute		
14a	Adaxial leaf surface hairy but without tooth-like hairs and tubercules		
	Adaxial leaf surface with only tooth-like hairs often associated with tubercules		
14b	Branch indumentum with geniculate antrorse hairs and sessile glands occasional to absent, pherophylls ovate, glandular hairs absent on reproductive material		
	Branch indumentum with patent or spreading hairs and regularly distributed sessile glands, pherophylls hastate, glandular hairs present at least on calyx		
39	Leaves 8–20 mm long, glandular hairs on calyx		
	Leaves 7–24 mm long, lacking glandular hairs on calyx		

39a	Stems densely hairy, leaves hairy on adaxial surface	P. decussata
	Stems sparsely to moderately hairy, leaves with adaxial surface glabrous	39b
39b	Stem trichomes spreading, flowers appearing axillary and with darks spots in corolla throat	P. howelliae
	Stem trichomes antrorse, flowers in racemose inflorescences (rarely appearing axillary) and without markings in corolla throat	P. denticulata

Acknowledgments

We thank Catherine Wardrop (NSW) for botanical illustrations. We thank previous owner (Mrs D. Horton), and current owners (Anthony and Brenda Smith; David Schlunke) for access to their property to assist us with collections of *P. crocodyloides*. Darren Shelly (Office of Environment & Heritage) and Matt Renner (NSW) assisted with collecting, assessing specimen and population data, and provided field assistance. David Egan (National Parks Wildlife Service Griffith), David Albrecht (ANH), James Schlunke and Guy Taseski (NSW) assisted with references, location of specimens and helpful suggestions on the manuscript. Tony Orchard provided detailed information, transcripts and advice relating to Allan Cunningham's history and collections. Loans and specimens were kindly provided by K, NSW and CANB. Peter G Wilson (NSW) and two anonymous reviewers provided helpful comments that greatly improved the manuscript. Trevor Wilson was supported by the *Australian Biological Resources Study* (ABRS) grant (RFL212-43).

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